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AXILLARY CLEISTOGENES IN SOME AMERICAN GRASSES

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A few years ago a previously unknown form of cleistogene was discovered in autumnal specimens of *Triplasis purpurea*.¹ These were solitary, sessile, single florets without glumes, and were borne in the lower sheaths, clasped in the wings of an indurate prophyllum (fig. 1). It was noted that specimens bearing these cleistogenes readily disjointed at the nodes. With this character and a slight swelling above the nodes as clues, other examples were sought from time to time with the result that some twenty more grasses were found to produce similar cleistogenes. They are produced by all the species native in the



FIG. I. Triplasis purpurea. Ordinary spikelet (chasmogene) and cleistogene and grain of each— \times 5.



FIG. 2. Danthonia spicata. Ordinary spikelet and cleistogene, with subtending prophyllum, and grain of each—× 5.

United States of three genera, Triplasis with three species, Danthonia with twelve, and Cottea with one. They are also found in *Muhlenbergia microsperma* and in *Pappophorum Wrightii*. In all cases the cleistogenes, borne at the lower nodes of flowering culms and not in leafy shoots, are strikingly different from the chasmogenes (that is,

¹ See Bot. Gaz. 45: 135-136. 1908.

the spikelets borne on the terminal panicle) of the same plant. Often, if their source were unknown, they would not be placed in the same tribe. The characters that are common to all are simplified structure and enlarged grain. In Triplasis the prophyllum is enlarged and indurate, and enfolds the entire spikelet; in Danthonia it is thin in texture, is split to the base, and simulates a pair of narrow glumes. (Repeated dissections have been made to decide whether these organs are parts of a prophyllum or a pair of glumes. In the very few immature spikelets found they are evidently prophylla, but immature spikelets are very difficult to find. The keels are ciliolate as are the prophylla, instead of glabrous as are the glumes of the chasmogenes.)

The type of spikelet characteristic of the genus Danthonia is shown in the sketch of Danthonia spicata, our commonest species (fig. 2). The two long glumes exceeding the several crowded florets, the short rachilla joints, and the 2-toothed lemma bearing a flattened awn tightly twisted below, are the distinguishing characters of the genus. cleistogenes are all without glumes. In Danthonia spicata there is but one floret, sometimes with a slender rachilla joint bearing a minute rudiment of a second floret. The lemma is not toothed; it is usually merely pointed, but a few have been found with the point slightly lengthened, flattened, and somewhat twisted. (Note the relative size and shape of the grains). In some of the other species, especially the western Danthonia intermedia, D. americana, and D. californica, there are commonly two, three, or four widely separated florets, with slender rachilla joints almost as long as the florets, forming a striking contrast to the crowded florets characteristic of the genus. lemmas are entire and awnless, or awn-tipped as in D. spicata. genus Danthonia comprises something over 100 known species, Africa being the home of more than half of them. All the material of the genus in the National Herbarium was examined. (The examination, because it necessitates some injury to the specimens, was by no means thorough.) The one Mexican and two West Indian species show no sign of cleistogenes; their wiry junciform habit would not lead one to expect them. Of the South American species, four, Danthonia chilensis, D. cirrata, D. montevidensis, and D. picta, were found with cleistogenes. But only one species from the eastern hemisphere, Danthonia semiannularis of New Zealand, was found to produce them. From our own species it would appear that these cleistogenes are produced after the maturity of the panicled spikelets. In Danthonia

spicata few herbarium specimens reveal these cleistogenes, but if the curly tufts so common in late autumn on sterile knolls and rocky hillsides be examined they are invariably (in my experience) found with cleistogenes in the broken culm or in the internodes remaining in the tuft. I surmise they are a regular rather than an occasional method of reproduction.

The chasmogamous spikelet of Cottea pappophoroides is a highly specialized one, the florets being deeply 5- to 7-cleft and awned, and partly hidden in copious white hairs. The cleistogene is usually solitary, without glumes, and consists of a single floret with a length-



Fig. 3. Cottea pappophorand cleistogene and grain of let and cleistogene and each— \times 5.



Fig. 4. Pappophorum Ordinary spikelet Wrightii. Ordinary spikegrain of each-× 5.



Fig. 5. Muhlenbergia microsperma. Ordinary spikelet, cleistogene enclosed in subtending leaf, cleistogene removed, and grain of each— \times 5.

ened rachilla joint bearing a minute rudiment of a second floret. The lemma is sparingly silky villous and minutely awned or awnless (fig. 3; note the relative size and shape of the grains). The prophyllum is delicate and split as it is in Danthonia. In a single case a spike of three one-flowered spikelets was found. In these the second glume was developed, and this infolded the floret and rachilla joint.

In Pappophorum Wrightii the chasmogamous spikelet bears a

single perfect floret and two or three sterile florets, the lemmas of each being split into nine spreading plumose awns, all the awns together forming a feathery, pappus-like crown. The cleistogene, which is sometimes so rotund as to split the sheath in which it is borne, consists of a floret without glumes, and a rachilla joint with a minute rudiment of a second floret. The lemma is more or less split into a few closely appressed lobes (fig. 4; note the relative size of the grains). The prophyllum is thin in texture and is usually not split. In two cases the cleistogene was infolded in the sheath of a reduced leaf, so judged from its position opposite the prophyllum and from the clearly evident differentiation into sheath and blade. In one case a spike with three one-flowered spikelets was found. In two species of the eastern hemisphere cleistogenes were found, namely *Pappophorum boreale* from Transbaical, Siberia, and *Pappophorum brachystachyum* from the Algerian Sahara.

In Muhlenbergia microsperma the chasmogamous spikelet is very small, has minute glumes and a single long-awned floret. The cleistogene is usually awned, without glumes, and much more turgid than is the chasmogene (fig. 5; note the relative size of the grains). It is tightly folded in the swollen, spongy-indurate base of the sheath of a reduced leaf, which sometimes has a minute blade and ligule. In a few cases a tiny raceme was found with three or four spikelets with glumes like those of the chasmogenes. The cleistogenes are produced in abundance at the lower nodes, the subtending sheaths being pushed open by their bulk. (In old plants the numerous little cornucopias may be easily seen at the base.) The subtending prophyllum is membranaceous and remains attached to the nodes. Unlike those of Danthonia and the others, the nodes of M. microsperma do not disjoint, but the cleistogenes themselves readily fall at maturity. In Danthonia and the rest, the cleistogenes are permanently enclosed in the sheath together with the internode of the culm. (I surmise that the grains germinate within the sheath and push root and shoot through the internerves, but this has not been proved by experiment.)

In all the species in which these cleistogenes have been studied they are found to be more variable than are the chasmogenes of the same species. Only a limited study can be made in the herbarium, and as yet only Triplasis, Danthonia, and *Muhlenbergia microsperma* have been studied in the field. Notes from observers would be gratefully received. Since with relatively little study so many species have

been found to produce cleistogenes, it seems probable that this is not a rare habit in grasses. Any grass with swollen sheath bases and disjointing culms may repay examination, after the maturity of its terminal panicles. Most of the species so far found are plants of the arid regions or of dry places in the humid regions; all are plants of open ground.

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